

Germination Mode and Morphology of Seedlings in *Hanslia ormocarpoides* (Leguminosae)

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The germination mode and morphology of seedlings are described in *Hanslia ormocarpoides* (DC.) H. Ohashi (Leguminosae-Papilionoideae-Desmodieae). The seedling represents cotyledons enclosed by pericarp and testa and located at the ground-level, which corresponds to a cryptohypogeal or cryptogeal type of germination in Leguminosae. This germination mode is infrequent in the tribe Desmodieae, and *Hanslia* is the second genus that represents the germination mode in the tribe subsequent to the genus *Hylodesmum*. The first and second foliage leaves (eophylls) subsequent to cotyledons are predominantly borne in opposite pairs as with almost all other seedlings known so far in the tribe. Characteristic hairiness of the seedling was also mentioned.

Key words: Australia, cryptogeal germination, cryptohypogeal germination, Desmodieae, Desmodium, eophyll, germination mode, *Hanslia ormocarpoides*, Leguminosae, seedling.

The genus *Hanslia* Schindl. is distributed in Malesia, Papuasia (centred in New Guinea), Vanuatu and Australia (N. Queensland) (Ohashi 2005) and comprises two species, *H. hentyi* (Verdc.) H. Ohashi and *H. ormocarpoides* (DC.) H. Ohashi (Ohashi 2004, 2005). This genus is attributed to the tribe Desmodieae of subfamily Papilionideae, and is characterized by having a disk around the base of pistil, a lateral stigma, a scarcely developed rim-aril of the seed, loments composed of long and slender articles with uncinat hairs and a coarser, reticulate sculpture on pollen grains (Ohashi 2004). The tribe Desmodieae is divided into three groups: the *Lespedeza* group, the *Phyllodium* group and the *Desmodium* group, and *Hanslia* is included in the *Phyllodium* group

on the basis of morphological evidence without molecular data (Ohashi 2005). *Hanslia* is known its morphological features mostly based on herbarium specimens, and lacks its biological and ecological features.

Studies of seedlings of the Leguminosae were pioneered by de Candolle (1825) and recently reviewed by Duke and Polhill (1981). The seedlings show great diversity in morphology and germination patterns across the family. Characteristics of the legume seedlings have often been used in delimiting taxa at different levels as well as suggesting evolutionary trends between taxa (e.g., Maekawa 1955, 1982, Ambrose 1967, Ohashi 1973, Baudet 1974, Nozzolillo 1977, 1985, Nemoto and Ohashi 1993, López et al. 1998,

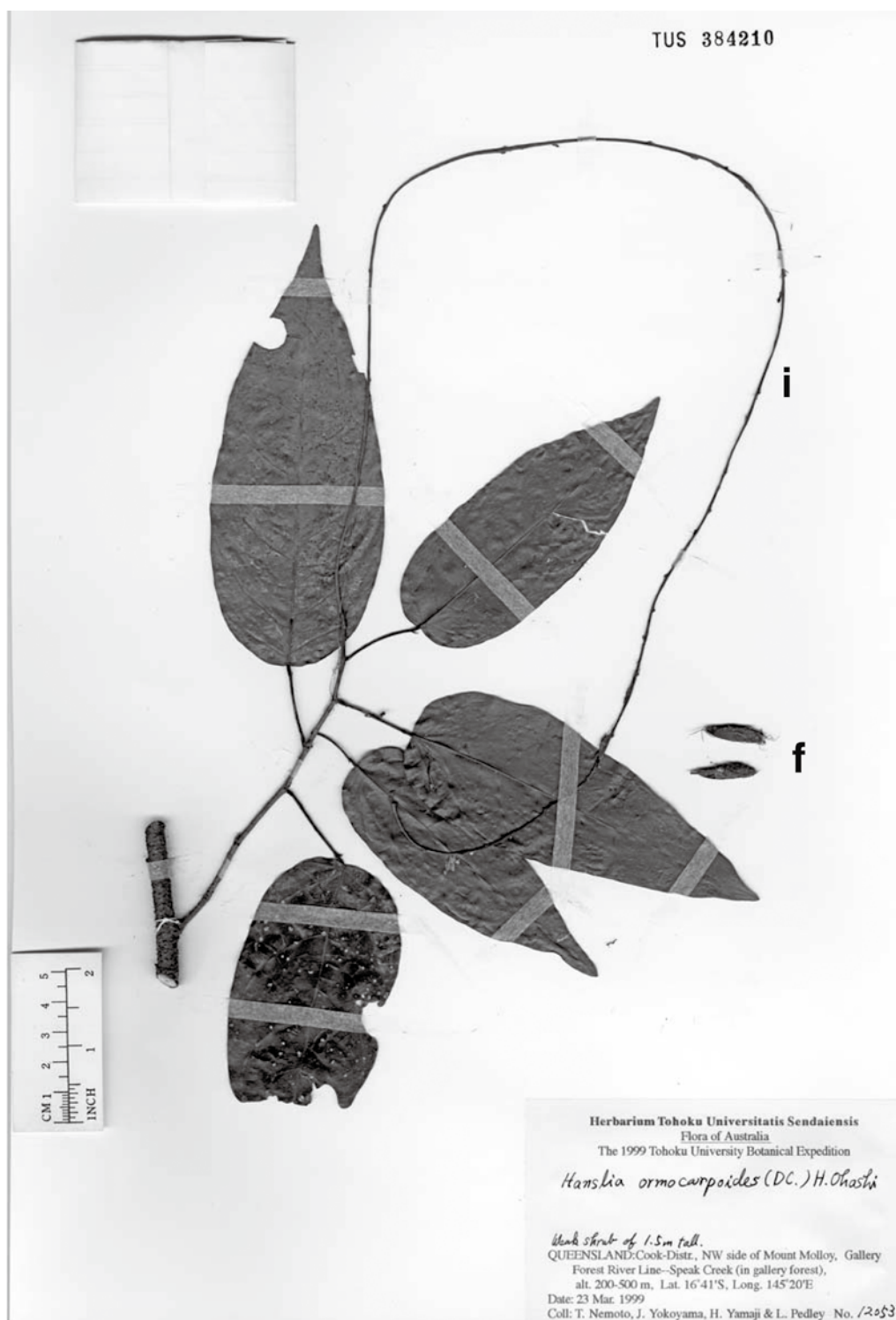


Fig. 1. *Hanslia ormocarpoides* (DC.) H. Ohashi, showing a branch terminating in a slender, elongated infructescence (i) and articles of jointed fruit (loment) (f). Voucher: T. Nemoto & al. 12053 (TUS).



Fig. 2. Seedling of *Hanslia ormocarpoides* (DC.) H. Ohashi, showing cotyledons enclosed by pericarp and testa and located at the ground-level, and the first two opposite leaves. Photograph taken at NW side of Mount Molloy, Cook Dist., Queensland, Australia on 23 March 1999.

Oliveira 2001, Rodrigues and Tozzi 2008). In the tribe *Desmodieae* two modes of germination are known, epigeal or hypogeal germination (Ambrose 1967, Ohashi 1973, Ohashi et al. 1981). Epigeal germination is common in the tribe, but the hypogeal one is found only in genera *Hylodesmum* as *Desmodium* (Ambrose 1967, Ohashi 1973). In addition, Clifford (1984) reported the seedling of *Hanslia* as cryptocotylar germination. In hypogeal germination the cotyledons remain enclosed within the testa and concealed beneath the surface of the soil, while the cotyledons burst through the testa and appear above the surface of the earth in the epigeal germination (von Denffer 1976). On the other hand, the term cryptocotylar is applied to the cotyledons remaining in the testa after germination in contrast to the cotyledons escaping the testa during germination (termed phanerocotylar) (Duke 1965). The hypogeal

germination found in *Hylodesmum* appears to be similar to the cryptocotylar one found in *Hanslia*. But the term cryptocotylar is applied whether or not the seed, or the cotyledons, is carried above ground during germination (Clifford 1984). The relative position of the cotyledons to the ground-level in *Hanslia* was uncertain, because Clifford (1984) just listed the name *Hanslia* as a genus representing cryptocotylar germination with no description or illustration.

In addition, the first few juvenile leaves of the seedling, called eophylls (Tomlinson 1960, Duke 1965, Duke and Polhill 1981), subsequent to the cotyledons have been known to represent variation in their arrangement in *Desmodieae*, i.e., opposite or alternate. In the genus *Desmodium* and allied genera (*Codariocalyx*, *Phyllodium* and *Tadehagi*) first two 1-foliolate leaves are opposite in all species examined in spite of difference in the mode of germination

(Ohashi 1973). De Vogel (1980) observed first 1-foliolate and second 3-foliolate leaves alternate in *Dendrolobium umbellatum* (as *Desmodium umbellatum*). In *Lespedeza*, two patterns, opposite and alternate, were recognized in the arrangement of eophylls in relation to disjunct distribution pattern of species between eastern Asia and eastern North America (Nemoto and Ohashi 1993). This character was assumed to have a phylogenetic background from molecular data (Nemoto et al. 2010, Han et al. 2010). However, no features of eophylls are known in *Hanslia*, although seedlings of several species of *Hylodesmum* have been described and illustrated in detail by Ambrose (1967) and Ohashi (1973).

Ohashi (1973) considered the hypogeal germination in *Hylodesmum* is adapted to temperate and subboreal regions and a more advanced mode than the epigeal one in *Desmodium* and allied genera. The hypogeal germination is also considered to be advanced generally in the angiosperms (Ehrendorfer 1976). Because *Hanslia* is distributed in tropical regions and has more primitive features in the tribe *Desmodieae* such as a floral disk and a coarser, reticulate sculpture on pollen grains (Ohashi 1973), the cryptocotylar germination similar to the hypogeal one was unexpected in the genus. The seedlings of *Hanslia* must therefore, be observed in detail.

Hanslia ormocarpoides is found in Malesia (Lesser Sunda Is., Maluku, New Guinea, Philippines, Sulawesi), Australia (central to northern Queensland coast) and Southwestern Pacific (Solomon Is. and Vanuatu) (Pedley 1999, Ohashi 2004, 2005), while *H. hentyi* from New Guinea and Borneo (Verdcourt 1979, as *Desmodium hentyi* Verdc.; Ohashi 2004). The former species has 1-foliolate leaves and leaflets round at base, while the latter (1–)3-foliolate leaves and leaflets acute at base. In 1999 we performed a field expedition in north-eastern Queensland, Australia for collecting legume plants. Near Mount Molly in Cook District of Queensland, we collected some plants of *Hanslia*

ormocarpoides bearing 1-foliolate leaves and terminal infructescences with a few mature fruits (Fig. 1), one young plant of ca. 10 cm tall of which cotyledons and some subsequent leaves had already disappeared, and 10 seedlings (Figs. 2, 3). The plants with infructescences were shrubs of ca. 1.5 m tall, and they grew along the side of a small stream covered by the canopy of trees grown on both sides of the stream. Because they were partly covered with dried mud or dried fragments of plants, they appeared washed wholly by floods before. In the western suburb of Cairns in Queensland, we found some young plants of the species less than 12 cm tall and nine seedlings on the side of a road passing through a shady forest.

Our knowledge on the mode of germination and seedling morphology is still limited in tribe *Desmodieae*. In this paper, the germination mode and morphology of seedlings of *Hanslia ormocarpoides* (DC.) H. Ohashi are described and illustrated based on specimens collected by ourselves in order to supplement seedling data of tribe *Desmodieae*.

Description of seedling morphology

The seedling of *Hanslia ormocarpoides* show that the cotyledons remain within the pericarp and testa without escape from them and they are located on the soil, or at ground-level in or little above the soil litter without lifting off the ground by the hypocotyl (Fig. 2). Subsequent to the cotyledons there are two opposite 1-foliolate leaves, or eophylls, in most seedlings collected (Figs. 3A, C, D, F, G, 4A), but they are alternately borne in a few individuals (Fig. 3E). Because the adult leaves, or metaphylls, of *H. ormocarpoides* are 1-foliolate, there are no clear distinctions in shape between the eophylls and the metaphylls except for opposite or alternate phyllotaxis. The opposite phyllotaxis is characteristically found only in seedling stage and, therefore, here we regarded the first two foliage leaves as eophylls. The eophylls are more broadly ovate in shape than the subsequent

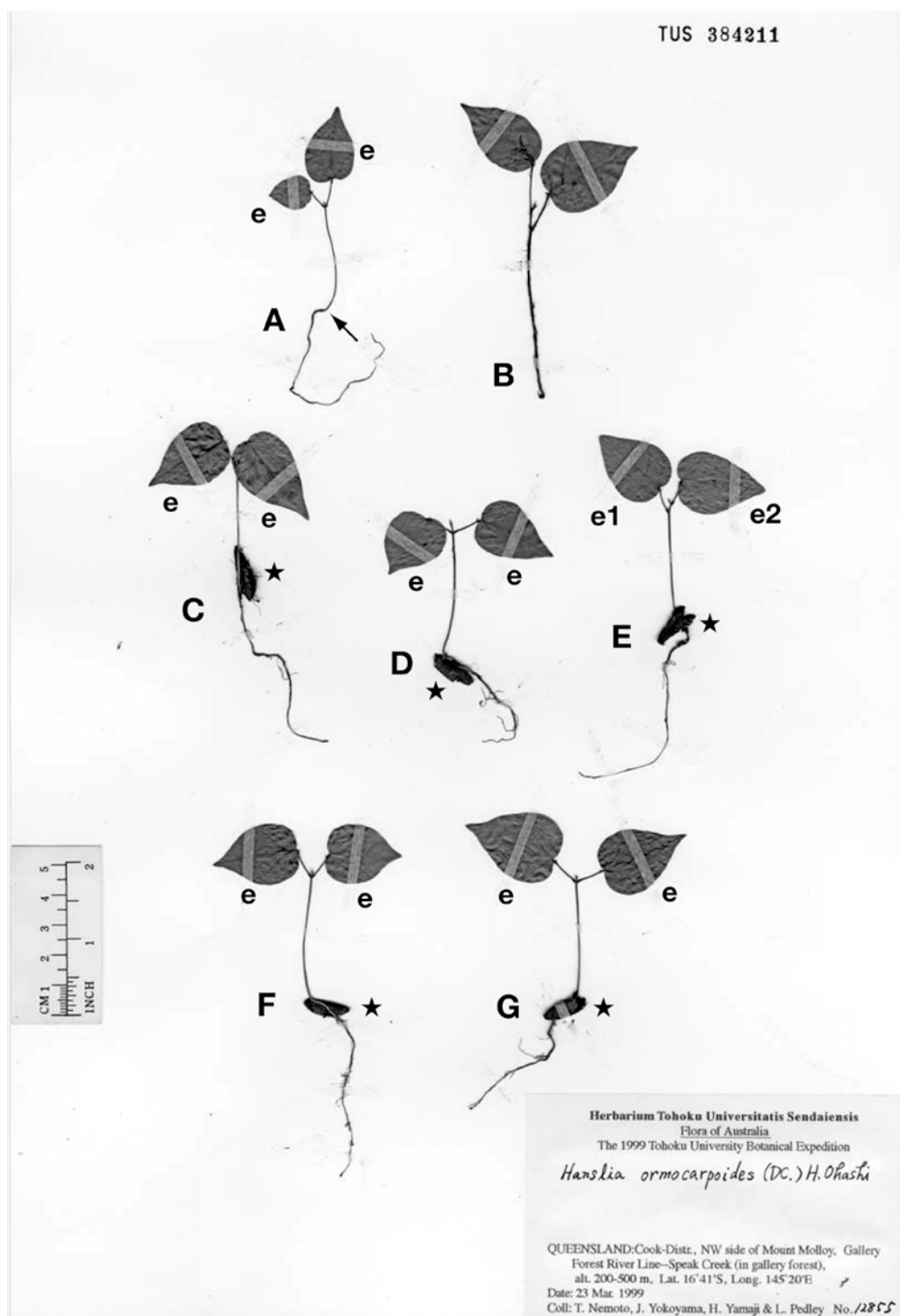


Fig. 3. Seedlings (A, C–G) and young plant (B) of *Hanslia ormocarpoides* (DC.) H. Ohashi, showing cotyledons enclosed with pericarp and testa (asterisks), the original position of cotyledons in A (arrow), and cotyledons turned upward artificially when making specimen in C. e. Opposite ephylls. e1, e2. Alternate ephylls. Voucher: T. Nemoto & al. 12855 (TUS).

metaphylls that become increasingly narrower and elongated. The eophyll has two stipules at the base of the petiole and they appear to be unstable in their form and represent the following variations: when two eophylls are opposite, their stipules are connate in pair (Fig. 4B) or partly connate with two-lobed apex (Fig. 4C); when the two eophylls are alternate, each has their own two stipules (Fig. 4D). Because most seedlings collected were in the stage with two leaves (eophylls) and only two seedlings had three leaves, we described until the third leaf stage here. Details of seedling morphology are described below:

Cotyledons hypogeal or geal, remaining within testa and pericarp, narrowly ovate, entire, $13.5\text{--}19.5 \times 3\text{--}4$ mm, puberulent beneath at the base; testa membranous, dark brownish; pericarp surface with uncinata hairs. Hypocotyl 10–15 mm long, puberulent mixed with uncinata hairs. Epicotyl 25–58 mm long, spreading- or ascending-puberulous with brownish hairs slightly mixed with unicate ones. First two leaves (eophylls) opposite (infrequently alternate in three of 19 seedlings), stipulate, petiolate, stipellate, 1-foliate. Stipules on the same side of stem fused into one and with one midrib, narrowly triangular, or variously fused at the base and with two-lobed at the apex and with two midribs, $1.6\text{--}2.5 \times 0.2\text{--}0.3$ mm, appressed- or ascending-puberulent on the outside and along the margin. Petioles 8–13.5 mm long, with two ridges on the upper side, hairy like the epicotyle; pulvini 1–1.5 mm long. Leaflets with two stipels at the base of the leaflet-pulvinus, $15.5\text{--}34 \times 9.5\text{--}23.3$ mm, ovate to broadly ovate, acuminate at the apex, subcordate at the base, entire along the margin, glabrous or sparsely appressed-puberulous with brownish hairs on the midrib and lateral veins above, the midrib and lateral veins below appressed- or ascending-puberulous with brownish hairs, reticulate veins and the intervein area sparsely puberulent with spreading or ascending tiny hairs, lateral nerves not reaching the margin, the margin

sparsely ciliate with pale brownish hairs; stipels subulate, $0.8\text{--}1.8 \times 0.1\text{--}0.2$ mm long, hairy like the stipules; leaflet-pulvinus 1.4–2 mm long, hairy like the petiole-pulvinus. The third leaf subsequent to the eophylls $27\text{--}39.5 \times 16.5\text{--}24$ mm, shape and hair like the eophylls, but slightly larger and narrower; petiole 12–16 mm, hairy like the eophylls.

Specimens examined: AUSTRALIA. Queensland, Cook Distr.: NW side of Mount Molloy, Gallery forest River Line – Speak Creek (in gallery forest), alt. 200–500 m, $16^{\circ}41'S$, $145^{\circ}20'E$, 23 March 1999, T. Nemoto, J. Yokoyama, H. Yamaji & L. Pedley 12053 (adult plants), 12855 (young plants and seedlings) (TUS); W side of Cairns, along roadway from State RD 91 to Lake Morris, alt. 100–300 m, $16^{\circ}57'S$, $145^{\circ}43'E$, 24 March 1999, T. Nemoto, J. Yokoyama, H. Yamaji & L. Pedley 12742 (young plants and seedlings) (TUS).

Remarks

The mode of germination observed in *Hanslia ormocarpoides* corresponds to cryptohypogeal or cryptogeal type in *Leguminosae* (Duke and Polhill 1981) as well as *Heliciopsis* type/subtype (de Vogel 1980) or cryptocotylar-hypogeal-reserve (CHR) type (Garwood 1996). Clifford's (1984) observation on the germination mode in *Hanslia* was confirmed by our observation as well as the hypogeal or geal position of cotyledons enclosed by testa and pericarp. This is the second case of cryptocotylar and hypogeal or geal type of germination recognized in the tribe *Desmodieae* following *Hylodesmum* (Ambrose 1967, Ohashi 1973). De Vogel (1980, p. 120, Table 10) mentioned the seedling type of *H. ormocarpoides* (as the subgenus *Hanslia* under genus *Desmodium*) as 'Sloanea type/subtype (2a)', which corresponds to a phaneroepigeal mode of germination, based on Ohashi (1973). However, this was incorrect citation of Ohashi (1973) in which the seedlings of the species was not examined and mentioned.

The tribe *Desmodieae* is divided into three groups, the *Lespedeza*, *Phyllodium* and *Desmodium* groups (Ohashi 2005). Although *Hanslia ormocarpoides* is attributed to the *Phyllodium* group, the cryptohypogeal or

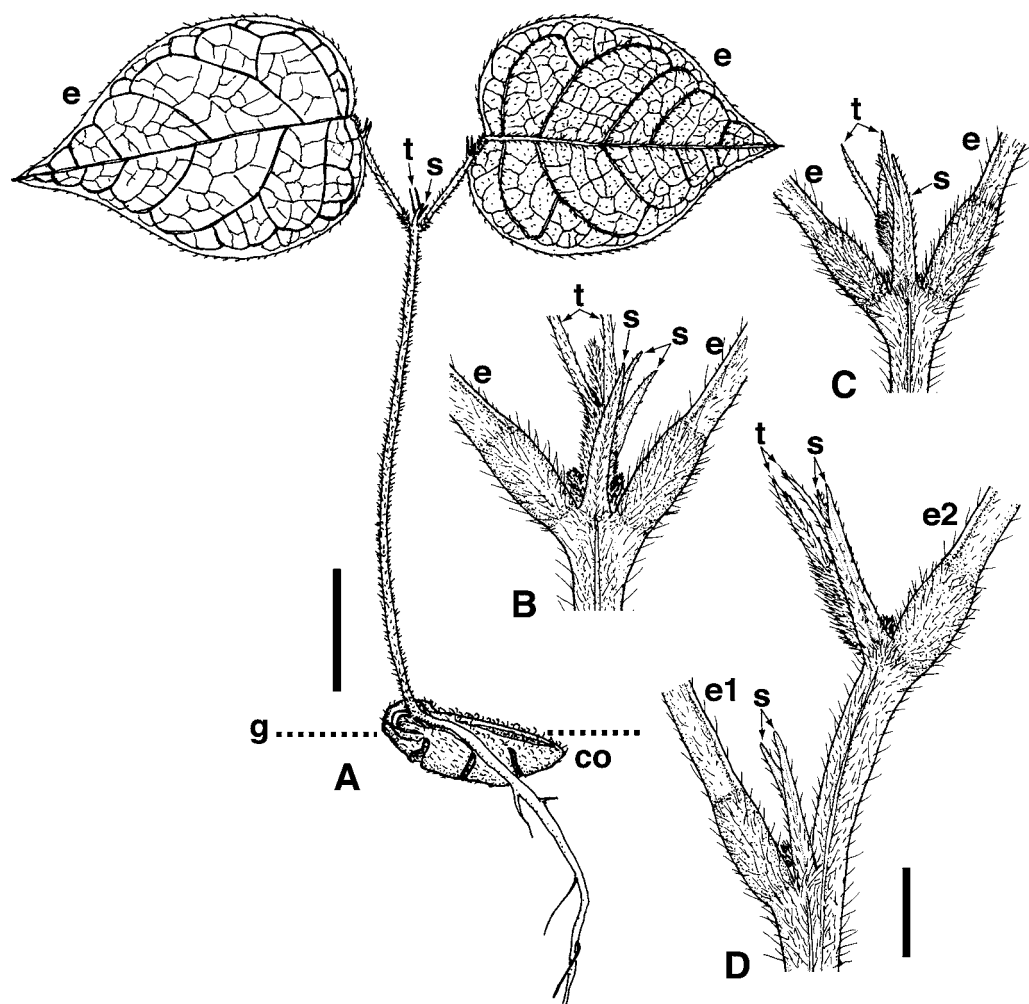


Fig. 4. Seedlings and variation of stipules at nodes of eophylls of *Hanslia ormocarpoides* (DC.) H. Ohashi. A. Illustration of Fig. 3F, showing puberulent epicotyl, petioles and leaflets (margin and lower surface) of eophylls. B. Node of eophylls in A, showing completely connate stipule (this side) and bifid one (the other side) shared by two eophylls. C. Node of eophylls in Fig. 3A, showing a bifid stipule. D. Two nodes of alternate eophylls of Fig. 3E, showing each eophyll with two stipules. co. Cotyledons enclosed with pericarp and testa. e. Eophylls opposite. e1 and e2. Eophylls alternate. g. Ground-level. s. Stipule. t. Two stipules of the third leaf (undeveloped) subsequent to two eophylls. Scale bars: 1 cm (A), 1 mm (B–D).

cryptogeal type of germination is similar to that of *Hylodesmum* (Ohashi 1973, as *Desmodium* subgen. *Podocarpium*) of the *Desmodium* group. In the *Phyllodium* group the mode of germination has been examined only in limited species of the genera *Phyllodium*, *Ohwia*, *Tadehagi* (Ohashi 1973) and *Dendrolobium* (de

Vogel 1980, as *Desmodium umbellatum*) and was a phaneroepigeal type in all of these species. Even in the *Lespedeza* and *Desmodium* groups the phaneroepigeal type is common except for *Hylodesmum* in the *Desmodium* group (Ohashi 1973, Ohashi et al. 1981, Nemoto and Ohashi 1993). The cryptohypogeal or cryptogeal type

of germination appears to be independently evolved in the *Phyllodium* and *Desmodium* groups. Whether the mode of germination is characteristic for the genus *Hanslia* or not, we need information about the other species of the genus, *H. hentyi*.

In *Hanslia ormocarpoides* the stem was described as ‘glabrescent and young parts sparsely clothed with spreading minute uncinat hairs and with appressed short soft hairs’ (Ohashi 1973). However, the stem, or epicotyl, of seedlings are densely clothed with spreading or ascending hairs as well as uncinat ones, which is also one of characteristics of the seedling distinct from the young parts of the adult shoot. In addition, although the leaflets were described as glabrous below (Ohashi 1973, Verdcourt 1979), the plants we collected from northeastern Australia have sparsely minute hairs on the intervein area of the leaflet below in both seedlings and adult plants. The hairiness appears to be stable on the course of development of the plant.

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根本智行^a, 大橋広好^b: マメ科 *Hanslia ormocarpoides* における芽生えの発芽様式と形態

1999年3月にオーストラリアで実施したマメ科植物の調査の際、クイーンズランド州北東部のケアンズ近郊および近隣で *Hanslia ormocarpoides* (DC.) H. Ohashi の果実をつけた個体と幼植物および芽生え個体を採集した。発芽様式と芽生え形態はマメ科では分類形質としてしばしば注目されてきたが、本種については Clifford (1984) によって子葉が種皮に包まれる *cryptocotylar germination* であることが報告されているのみで、葉序や形態など芽生えの詳細な特徴についてはこれまで記載されてこなかった。そこで、本論文では現地での観察と採集した標本に基づいて、本種の発芽様式と芽生え形態を記載した。

本種の芽生えの子葉は、Clifford の報告通り、果皮および種皮に包まれたままであった。さらに、現地での観察から子葉は地表にわずかに覆われているか、あるいは、ほぼ地表面に位置していることが判明し、これは地下性あるいは地表性の発芽様式、すなわち、*cryptohypogeal* あるいは *cryptogeal type* (Duke and Polhill 1981), *Heliciopsis type/subtype* (de Vogel 1980), *cryptocotylar-hypogeal-reserve* (CHR) type (Garwood 1996) とよばれる様式に相当する。本種の

帰属するマメ亜科ヌスビトハギ連では、発芽時に子葉は果皮および種皮を脱ぎずて地上で2枚が葉状に展開する、いわゆる地上性の発芽様式 (*phaneroepigeal type*, *Sloanea type/subtype*, あるいは *phanerocotylar-epigeal-foliaceous* (PEF) type) に相当) が一般的に知られている。本種にみられる発芽様式は、ヌスビトハギ連では唯一ヌスビトハギ属 *Hylodesmum* にのみ知られており、*Hanslia* は2例目となる。ヌスビトハギ属と *Hanslia* はヌスビトハギ連では異なる系統群に属すると考えられていることから、発芽様式の類似は平行進化によって生じたものと考えられる。子葉に続く2枚の葉(初生葉)の形態と葉序(対生 vs. 互生)も芽生え形態の重要な形質であり、本種は2枚が対生(まれに互生)につくヌスビトハギ連で一般的な葉序をもつ。また、2枚の初生葉の托葉は、完全に合着するものから不完全に合着し、先端が二裂するものまで変化する。その他、芽生えの下胚軸、上胚軸、および初生葉の葉柄には開出あるいは斜上する短毛が密生し、これにかぎ毛が混生するという特徴がみられる。

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